

***Triathrix montagni* and *T. kalki*, a new genus and two new species of
Cletodidae (Crustacea: Copepoda: Harpacticoida) from California
and the Gulf of Mexico**

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Abstract.—*Triathrix* new genus (Copepoda, Harpacticoida, Cletodidae) is established to accommodate *T. montagni* new species from the California continental shelf and *T. kalki* new species from the Gulf of Mexico. The genus is characterised by a triangular, sharply pointed rostrum; a chitinous extension bearing four socles on the posterior border of the cephalothorax; no socles on the preanal somite; a median tube pore on the operculum; seta I of the caudal ramus implanted posterior to seta II; antennal exopod with three setae; mandibular palp with five setae; maxillary coxal endite with one seta and basal complex with eight setae; maxillary proximal syncoxal endite with two elements, allobasal endite with a spine and two setae, endopodal setae not fused at base; maxillipedal syncoxa without seta; no sexual dimorphism on male P3; female P5 with baseoendopodal lobe and exopod long, rectangular and equal in length. The two species can be distinguished easily from each other by the size of the dorsal extension to the cephalothorax, the shape of the dorsal median socles on the free prosomites, the length of setae on the P1 and male P5 baseoendopodal lobe and the length to width ratio of the caudal rami and the female P5. *Enhydrosoma nicobarica* Sewell, 1940 is also included in the genus as *T. nicobarica* new combination.

Sewell (1940) described *Enhydrosoma nicobarica* Sewell, 1940 from a single immature specimen found in weed washings in Nankauri Harbour in the Nicobar Islands off the north coast of Indonesia. Within the genus *Enhydrosoma* Boeck this species is unique in that the exopod of the antenna has three setae: a large, plumose seta on the lateral margin along with a large, plumose and a small, naked seta on the distal margin. In his consideration of the genus, Gee (1994) dismissed *E. nicobarica*, in his preliminary assessment of the genus, on the grounds that it was a juvenile (copepodid V), although he considered that an antennal exopod bearing three setae was probably the plesiomorphic condition in Cletodidae

based on this condition being found in *Limnocletodes*, Borutsky and, reportedly, in *Acrenhydrosoma perplexa* (T. Scott, 1899). More recently, Fiers (1996) has shown that a trisetose antennal exopod also occurs in the copepodid I stage of *E. lacunae* Jakubisiak, 1933 (and other *Enhydrosoma* species) but the small distal seta is lost in copepodid II and subsequent developmental stages. He concluded, from this, that the antennal exopod structure of *E. nicobarica* is not a juvenile feature and that the species should be removed from *Enhydrosoma* and placed as *species inquirenda* within the family.

During recent monitoring studies of the effects of oil and gas platforms on the sur-

rounding benthic fauna on the Californian continental shelf (Hyland et al. 1990, Montagna 1991) and the northern part of the Gulf of Mexico (Montagna & Harper 1996), two new species of Cletodidae have been discovered which, in the adult, have an antennal structure exactly akin to that described by Sewell (1940) for *E. nicobarica*. In this paper, we describe these species and demonstrate that they, and *E. nicobarica*, should be placed in a new genus within the Cletodidae.

Methods

Before dissection the habit is was drawn, and body length measurements made, from whole specimens temporarily mounted in lactophenol. Specimens were dissected and the parts mounted in lactophenol under coverslips sealed with Bioseal. All drawings were prepared using a *camera lucida* on a Nikon Optiphot 20 differential interference contrast microscope. The terminology for body and appendage morphology follows that of Huys et al. (1996). Abbreviations used in the text and figures are P1–P6 for pereopods 1–6 exopod (endopod)-1(-2-3) to denote the proximal (middle, distal) segments of a ramus. Body length was measured from the base of the rostrum to the median posterior border of the anal somite (i.e., excluding the caudal rami).

Family Cletodidae T. Scott, 1904

Our concept of the Cletodidae is based on that defined by Por (1986) after he removed many of the genera included in this family by Lang (1948).

Triathrix, new genus

Enhydrosoma Boeck, 1872, p. 53 (part.)

Diagnosis.—Cletodidae. Body semi-cylindrical with well defined somites, tapering posteriorly without clear distinction between prosome and urosome. Cephalothorax with distinct chitinous extension on dorsal posterior margin carrying 4 sensillum-

bearing socles. Free-prosomes and urosomite-1 with 6 sensillum-bearing socles and 4 sensilla without socles, dorso-lateral socles usually very pronounced; urosomites-2 to -4 with 4 sensillum-bearing socles and 4 sensilla without socles. Female genital double-somite with a continuous cuticular rib marking line of fusion; genital field with vestigial P6s, bearing 1 seta, covering separate gonopores; minute copulatory pore adjacent to cuticular rib. Preanal somite without any socles. Urosomites, except anal somite, with a double row of spinules on ventral posterior margin and a pair of lateral tube pores; anal somite with additional pair of ventro-lateral tube pores, and single tube pore on operculum. Caudal rami much longer than wide, tapering posteriorly; minute seta I implanted posterior to seta II; seta III implanted more or less medially on outer margin and seta VII proximal to seta III on inner dorso-lateral margin; ventral and lateral tube pore present in median portion of ramus. Rostrum well-developed, distinctly triangular in shape with sharply pointed recurved tip. Female antennule 5-segmented; setal formula 1[1], 2[8], 3[8+aesthetasc], 4[1], 5[11+aesthetasc]. Male antennule 6-segmented. subchirocer; segment-4 swollen, with row of lanceolate setules but without modified setae; setal formula 1[1], 2[9+tube pore], 3[8], 4[13+aesthetasc], 5[2+tube pore], 6[9+aesthetasc]. Antennal allobasis with 2 pinnate setae on abexopodal margin; exopod a well-developed segment with 3 setae (1 pinnate seta on lateral margin and 1 pinnate and a small naked seta on distal margin). Labrum without central tuft of setules. Mandibular palp with 5 setae. Maxillary coxal endite with 1 seta; basis with 8 setae. Maxilla with 2 syncoxal endites, proximal endite with 2 elements, distal endite with 3 elements; allobasal endite with fused spine and 2 setae; endopod represented by 2 setae not fused at base. Maxillipedal syncoxa without seta; endopodal claw pinnate with a long accessory seta and a short finger-like projection at base. Male P3 without sexual

dimorphism. Setal formula of P1-P4 as follows:

	Exopod	Endopod
P1	0:0:022	0:0/111
P2	0:0:022	0:020
P3	0:0:122	0:021
P4	0:0:122	0:021

P5 exopod articulating with baseoendopod; in female endopodal lobe and exopod long, rectangular, equal in length and each with 3 setae; in male rami with 2 setae but endopodal lobe reduced. Male P6 a single asymmetrical plate without setae. Sexual dimorphism in antennule, P5, P6, urosome. Females with 1 egg-sac, males with 1 spermatophore.

Type species.—*Triathrix montagni* new species, by designation.

Other species.—*Triathrix kalki* new species and *T. nicobarica* (Sewell 1940) new combination.

Etymology.—The generic name is derived from the Greek noun *treis* (plural *tria*) meaning three and *thrix* meaning hair and refers to the condition of the exopod of the antenna.

Gender.—Feminine.

Triathrix montagni, new species.

Figs. 1–6C

Material examined.—Holotype, an adult female (dissected) USNM 278221; paratypes, 8 females (2 dissected) and 10 males (3 dissected) USNM 278822. All material collected by Dr. P. Montagna at CAMP site R4, 15 km off the central California coast, 34°43'N, 121°13'W, from a coarse silt sediment at approx. 90 m depth.

Female.—Body (Fig. 1). Length 0.59–0.67 mm (\bar{X} 0.62 mm, $n = 6$), almost cylindrical but flattened ventrally in urosome;

body surface glabrous. Cephalothorax tapering anteriorly, relatively deep dorso-ventrally; ornamented with sensilla and tube pores as in Fig. 1; anterior ventral borders with lateral extensions (Fig. 1A) slightly recurved dorsally (Fig. 1B); dorsal posterior border with large chitinous extension carrying 4 sensillum-bearing socles; lateral and ventral border with 14 sensilla. Posterior border of free prosomites and urosomite-1 with 6 sensillum-bearing socles and 4 sensilla without socles; dorso-lateral socles very pronounced, increasing in size posteriorly, each with an associated tube-pore. Genital double-somite with continuous median cuticular rib marking line of fusion, with 4 lateral sensillum-bearing socles and 2 dorsal sensilla; posterior border with, dorsally 2 sensilla, laterally 6 sensillum-bearing socles (ventral pair with an associated tube-pore) and, ventrally a double row of spinules and 2 sensilla (Fig. 2E). Urosomite-4 posterior border as for genital-double somite except that only 4 lateral sensillum-bearing socles. Pre-anal and anal somite without socles or sensilla except for a pair associated with smooth operculum (Fig. 1A); both somites with a pair of ventro-lateral tube pores; anal somite with additional pair of ventral tube-pores (Fig. 2C) and 1 tube pore on operculum (Fig. 1).

Rostrum (Figs. 1, 3E) well-developed, fused to cephalothorax, triangular, tapering to sharply pointed, strongly recurved tip; with 2 lateral sensilla but, apparently, no median ventral tube pore.

Caudal rami (Figs. 1, 2C) divergent, slightly swollen at base and tapering posteriorly; 4.1–4.4 times longer than maximum width; with tube pore mid-ventrally and laterally immediately posterior to seta III (Fig. 2C). Seta I inserted on ventro-lateral margin, posterior to seta II; seta III inserted laterally at 40% of ramus length; seta IV very small, fused at base to large seta V; seta VI small; triarticulate seta VII inserted at 28% of ramus length.

Genital field (Fig. 2D). Vestigial P6s extremely reduced with 1 seta. Gonopores

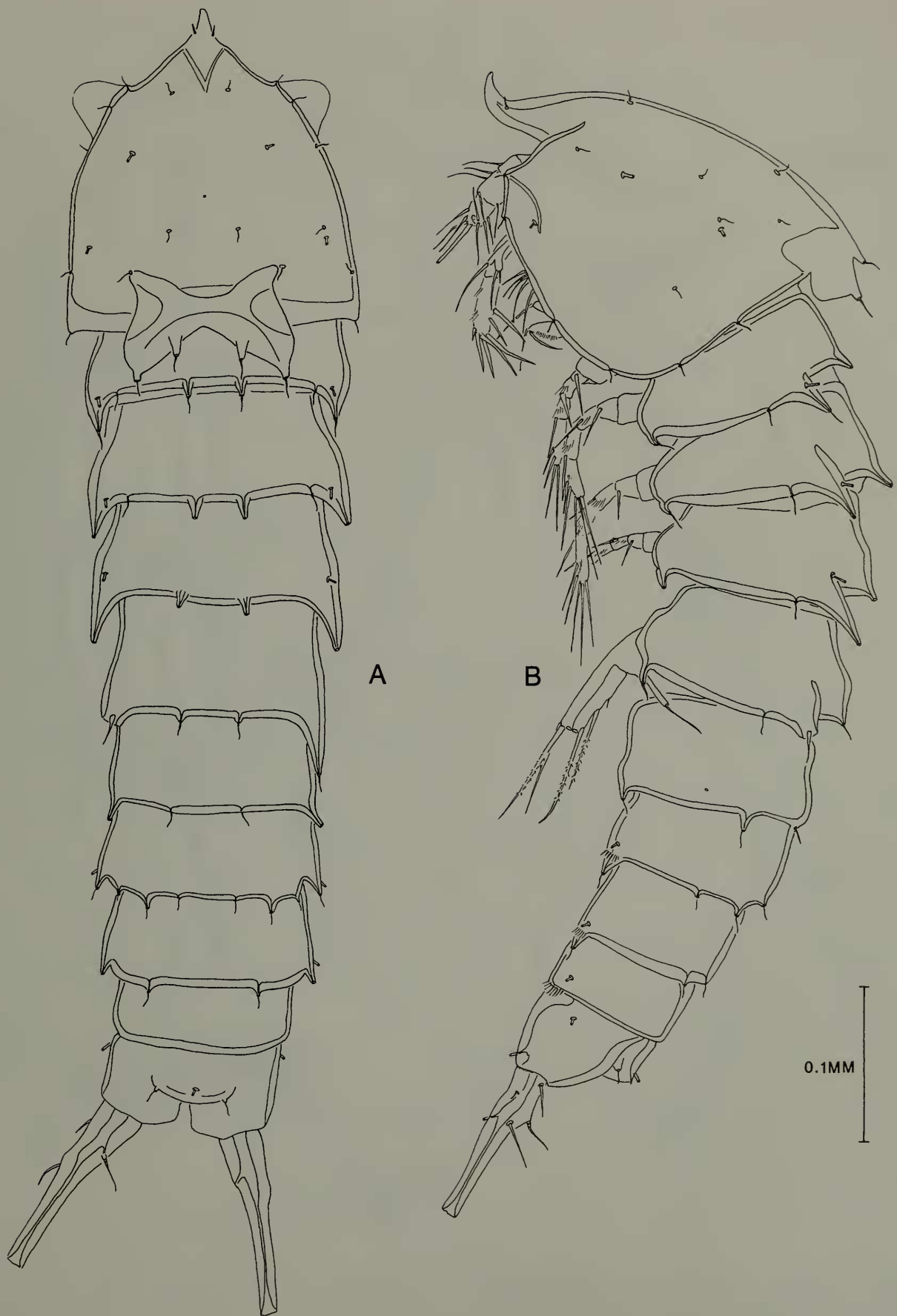


Fig. 1. *Triathrix montagni*, new species. Female body A, dorsal view; B, lateral view.

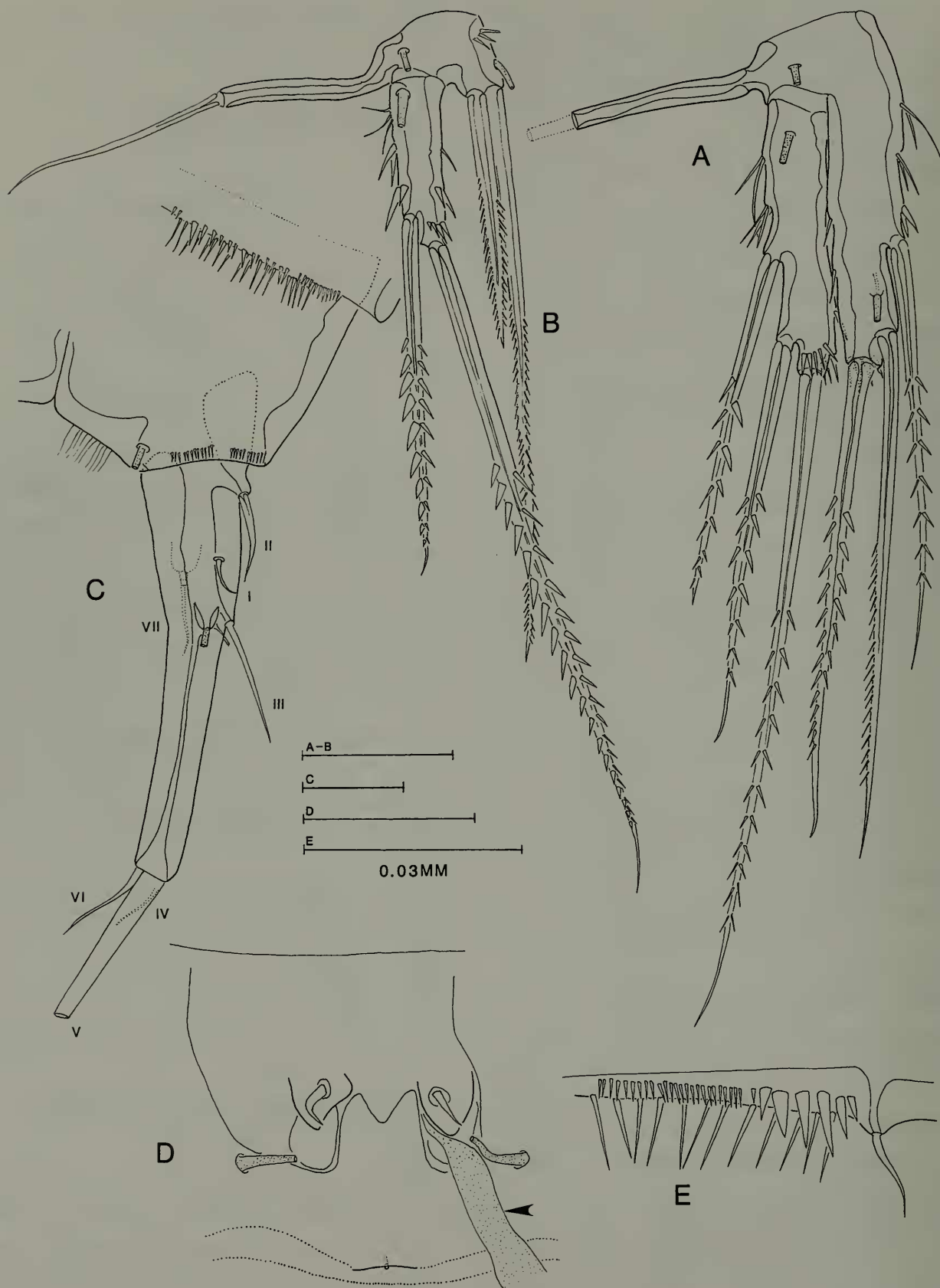


Fig. 2. *Triathrix montagni*, new species. A, female P5; B, male P5; C, female caudal ramus, ventral view; D, female genital field. E, portion of posterior border of female genital double-somite.

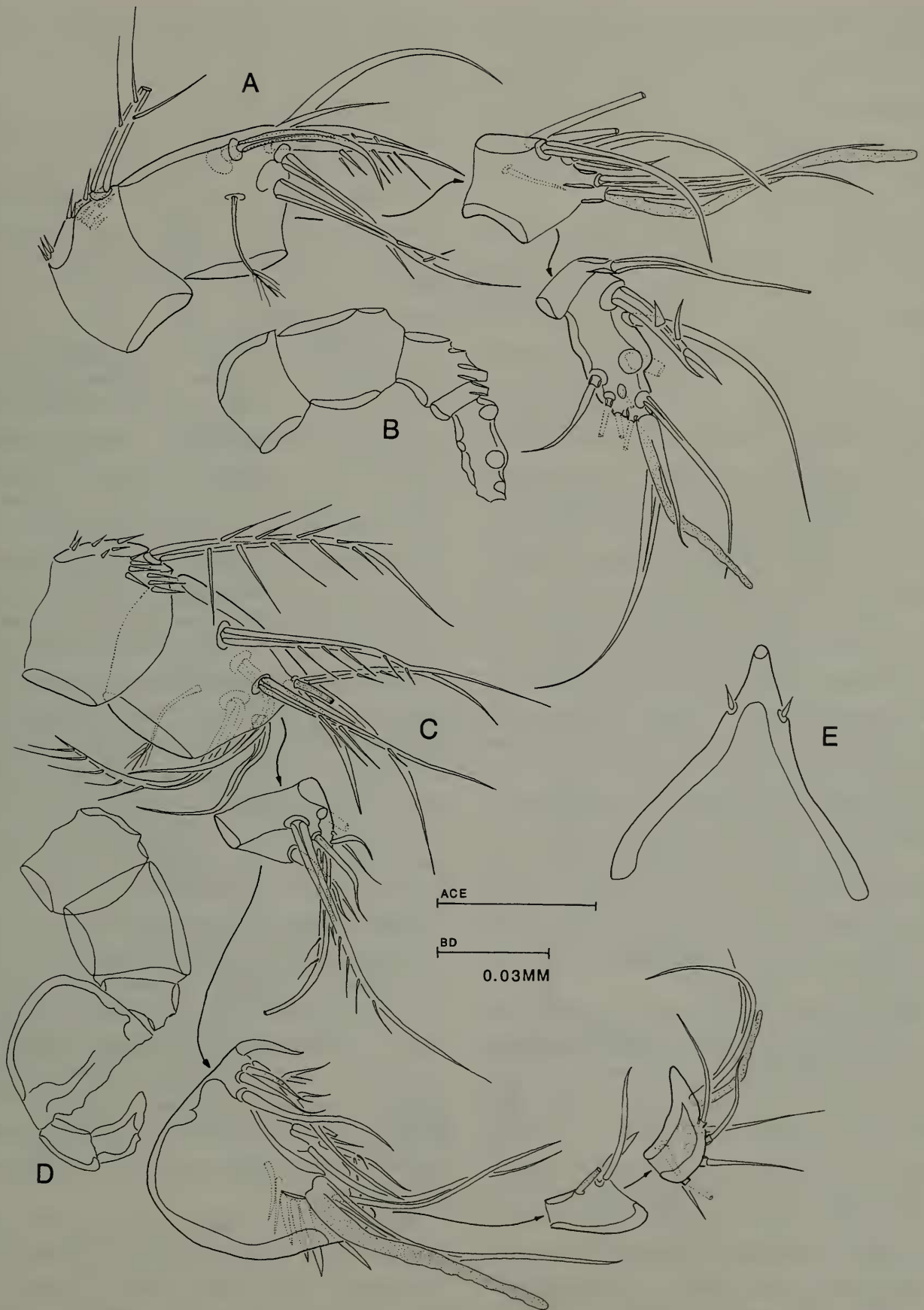


Fig. 3. *Triathrix montagni* new species. A, female antennule dislocated; B, female antennule segmentation only; C, male antennule dislocated; D, male antennule segmentation only; E, rostrum, dorsal view.

completely separate and under P6s (judging by attachment of remains of egg-sac arrowed in Fig. 2D). A pair of large tube-pores immediately posterior to gonopores. Copulatory pore well posterior near median cuticular rib, minute and maybe protected by integumental fold.

Antennule (Fig. 3A–B) short, stout, 5-segmented. Segment 1 with 3 rows of spinules and 1 large, bipinnate seta. Segment 2 with 4 pinnate and 4 naked setae. Segment 3 with 8 naked setae and an aesthetasc fused at base to one of setae. Segment 4 small with 1 naked seta. Segment 5 with 2 strongly pinnate setae and 7 naked setae on lateral margins; distal margin with a trithec of 2 naked setae and an aesthetasc.

Antenna (Fig. 4A). Coxa well-developed with row of setules. Allobasis with 2 strongly pinnate setae on abexopodal margin. Exopod well-developed, 1-segmented with row of setules round distal margin and with 3 setae (a large bipinnate seta on median lateral margin, a large bipinnate seta and a small naked seta in common socket on distal margin). Endopod with 2 rows of strong spinules on anterior margin and a dentate hyaline frill on posterior distal margin; armature consists of 2 spines and a seta subdistally and, on distal margin, 3 finely pinnate spines, 2 geniculate setae, a small seta fused to base of large inner spine, and a tube pore.

Mandible (Fig. 4B). Syncoxa robust with row of setules near base of palp; gnathobase with uni- and multi-cuspid teeth and 1 pinnate seta at distal inner corner. Palp well-developed, 1-segmented, with 5 bipinnate setae (3 on distal and 2 on inner margin).

Maxillule (Fig. 4C). Praecoxa with row of marginal setules; arthrite with 2 large tube setae on anterior surface, a row of setules on inner margin and, on distal margin, 4 cuspid teeth and a pinnate seta. Coxa well-defined with only 1 pinnate seta on distal margin. Basis with a row of spinules on anterior surface and 8 marginal elements (2 pinnate and 1 naked setae on distal endite, 2 naked setae on sub-distal endite, a

pinnate seta representing endopod, and a pinnate and a naked seta representing exopod).

Maxilla (Fig. 4D). Syncoxa with 2 marginal rows of spinules and 2 endites; proximal endite with 1 fused pinnate spine and 1 slender seta, distal endite with a fused pinnate spine and 2 naked setae. Allobasal endite with a fused pinnate spine and 2 naked setae. Endopod represented by 2 setae not fused at base.

Maxilliped (Fig. 4E). Syncoxa with 2 rows of spinules but no seta. Basis relatively short, oval, with a row of spinules on palmar and outer margin. Endopod represented by a minutely pinnate, recurved spine, a long, well developed accessory seta, and a small finger-like projection.

P1–P4 (Fig. 5) exactly same in both sexes (Fig. 5B–C). Intercoxal sclerites slender, curved. Protopods ornamented on anterior face as in Fig. 5, same in P1–P4 except that P1 basis with a strong bipinnate seta on inner margin and P2–P4 coxa with an extra row of small spinules centrally. Exopods 3-segmented, segments not elongate; P1 (Fig. 5A) with plain inter-segmental hyaline frills, P2–P4 with dentate frills; no tube pores on any segments; exopod-1 to 3 with 3 rows of spinules on outer margin, exopod-2 and -3 with a row of setules on inner margin; outer terminal seta of exopod-3 much longer than distal outer spine and 2 terminal pinnate setae with a comb of pinnules at tip. Endopods 2-segmented, endopod-2 much longer than endopod-1; both segments with spinules on outer margin, endopod-2 with setules on inner margin; P1 endopod-2 with 3 armature elements, middle one a pinnate seta with a comb-like tip (Fig. 5A).

P5 (Fig. 2A). Limbs well separated and connected by slender intercoxal sclerite (not illustrated). Small basal part of baseoendopod with a tube pore on anterior surface; outer margin with long pedicel bearing outer seta; endopodal lobe long, slender (4 times longer than wide), rectangular in shape and reaching to distal margin of exopod, with 3 rows of spinules on inner and

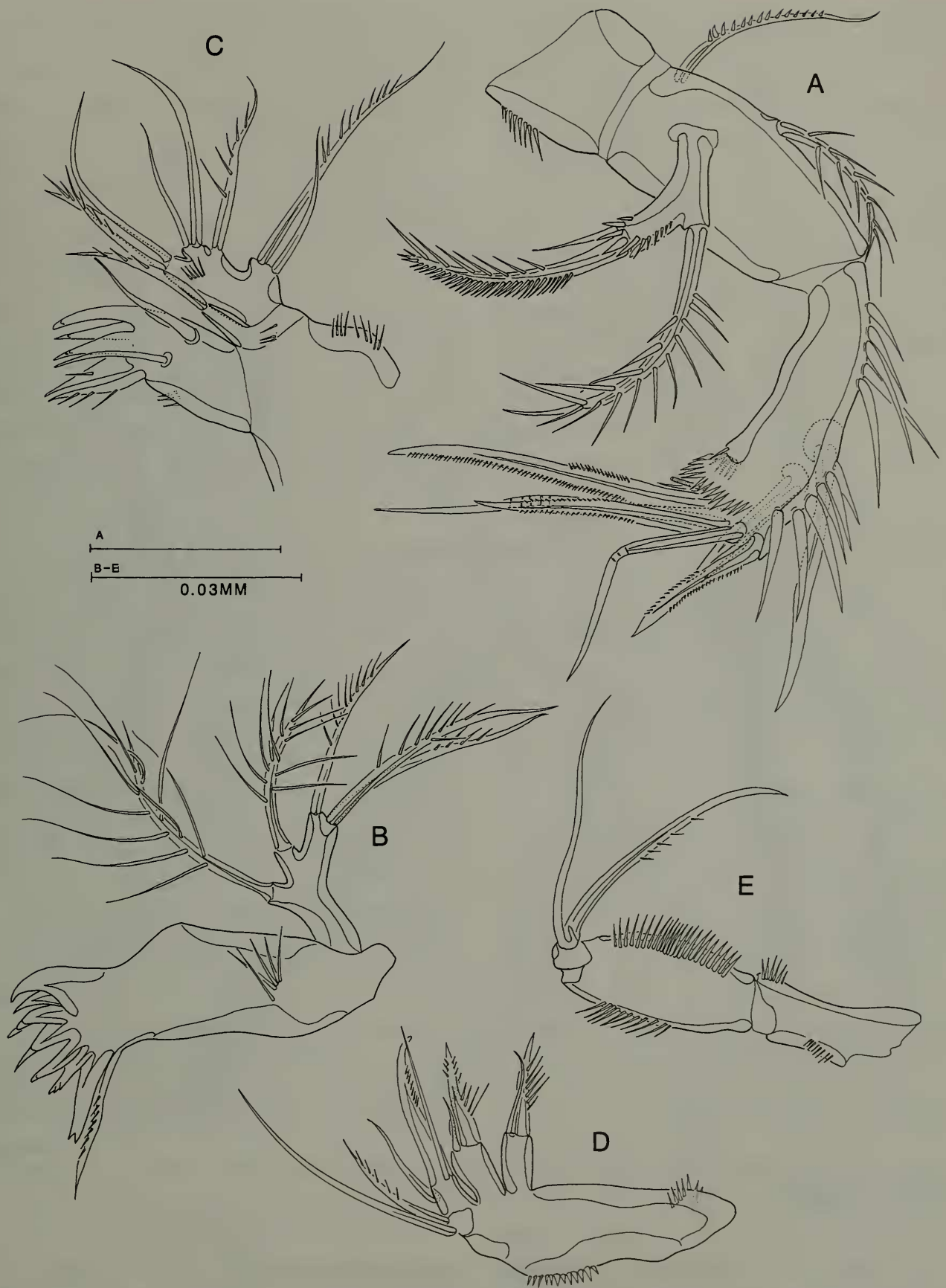


Fig. 4. *Triathrix montagni* new species. A, antenna; B, mandible; C, maxillule; D, maxilla; E, maxilliped.

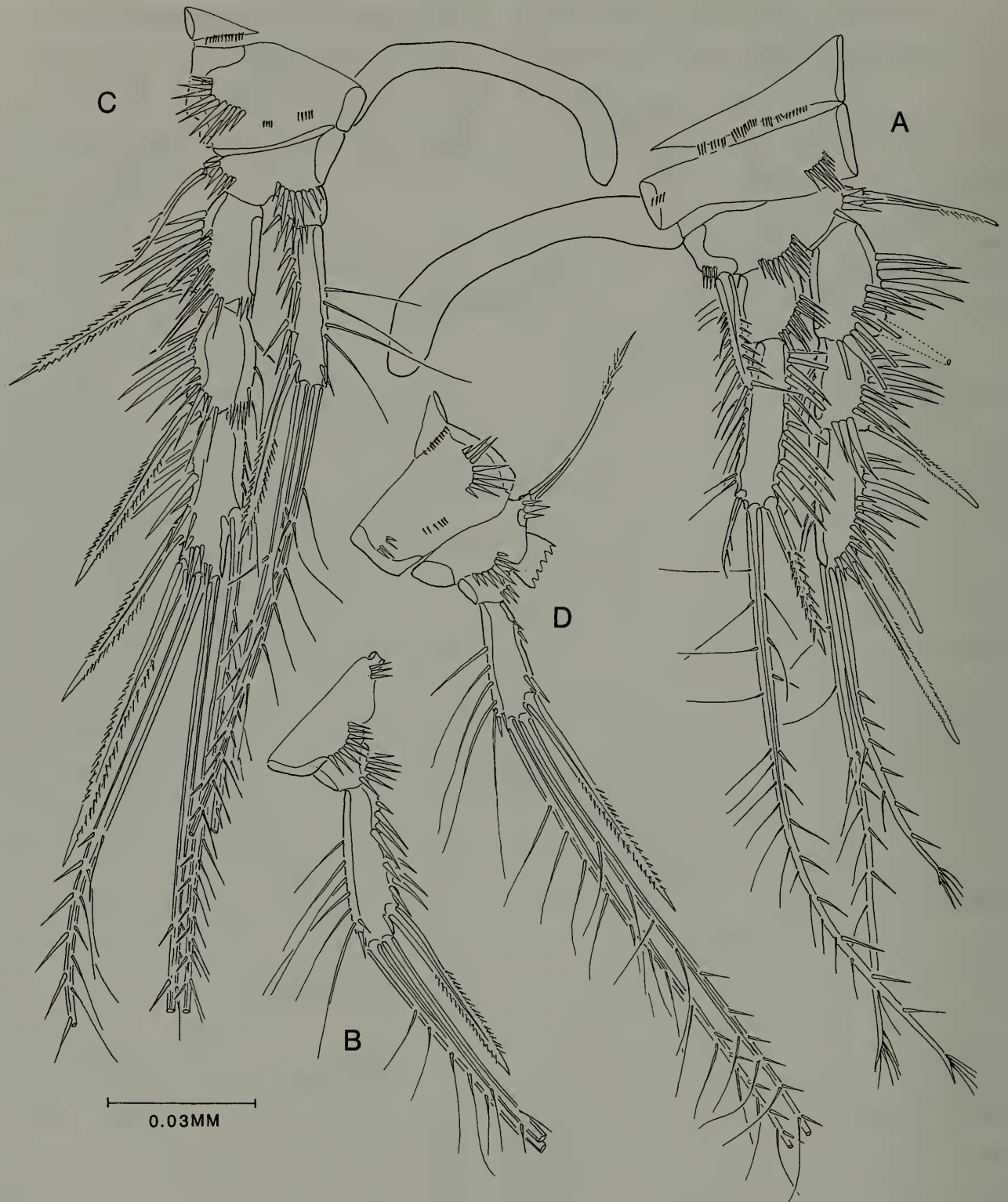


Fig. 5. *Triathrix montagni* new species. A, P1; B, female P3 basis and endopod; C, male P3; D, female P4 protopod and endopod.

outer margin, 1 row terminally on posterior surface, and tube pore on anterior surface between inner lateral and inner sub-distal seta; bearing 3 setae inserted and ornamented as in Fig. 2A. Exopod separate, articulating with margin of baseopod; long, slender (4 times longer than wide),

rectangular; ornamented with 2 rows of setules on outer margin, 1 row around distal margin, and a tube pore proximally on anterior surface; bearing 3 setae inserted and ornamented as in Fig. 2A.

Male.—As female except in urosome, antennule, P5 and P6.

Body (Fig. 6) length 0.60–0.71 mm (\bar{X} 0.64 mm, $n = 8$), slightly more slender than female. Urosomite-2 and -3 completely separate. P6 (Fig. 6C) on posterior margin of urosomite-2, an asymmetrical oval plate with row of small spinules but no setae.

Antennule (Fig. 3C–D) 6-segmented, sub-chirocer. Segment 1 with 3 rows of spinules and a large bipinnate seta on anterior margin. Segment 2 with nine setae (5 pinnate, 4 smooth) and a tube pore. Segment 3 with 8 setae ($\frac{2}{3}$? pinnate, $\frac{1}{3}$? smooth). Segment 4 strongly swollen with 13 setae and an aesthetasc fused to base of 1 seta on palmar margin; a row of strong setules on dorsal surface. Segment 5 with 2 setae and a tube pore. Segment 6 with a distal trithec and 7 other setae.

P5 (Fig. 2B). Elements well separated and connected by slender sclerite (Fig. 6C). Baseoendopod small, endopodal lobe virtually non-existent, with a tube pore on inner margin and 2 terminal setae, outer seta about half length of inner. Exopod separate, articulating with margin of baseoendopod, slender (3 times longer than wide), rectangular, with 3 rows of spinules on inner and outer margin and a tube-pore proximally on anterior face; with 2 bipectinate setae distally, outer about half length of inner.

Etymology.—This species is dedicated to our friend and colleague Dr. Paul Montagna who provided the specimens from his collections.

Variation.—Amongst the 19 specimens examined there was no variation in the structure and proportion of the appendages or the major features of the body ornamentation.

Triathrix kalki, new species
Figs. 6D–8

Material examined.—Holotype, an adult female (dissected) USNM 278223; paratypes, 4 females (1 dissected), 8 males (1 dissected) and 19 copepodids USNM 278224. All material collected by Dr. P. Montagna at Flower Gardens site, SE of

Galveston Texas, in the Gulf of Mexico, 27°54'N, 93°34'W, from a silty sand sediment at 110–160 m depth.

The following description is confined to those characters either not described for, or which differ from, *T. montagni*.

Female.—Body (Fig. 7A–B) length 0.44–0.54 mm (\bar{X} 0.51 mm, $n = 4$). Chitinous extension on posterior border of cephalothorax less pronounced and socles more equal in size than in *T. montagni*. Median dorsal sensillum-bearing socles on free prosomites and anterior urosomites fused together into Y-shaped structure, extended dorso-lateral socles without tube pore. Anal operculum (Fig. 8A) fringed with fine setules.

Caudal rami (Fig. 8A–B) slender, tapering posteriorly, 6 times longer than maximum width in ventral view. Setae II and VII inserted slightly more posteriorly (14% and 33% respectively) than in *T. montagni*.

Labrum (Fig. 8C). With a pore and small row of setules medially, oral margin with a short row of long spinules laterally and minute denticles medially.

P1–P4 (Fig. 8D–E). Outer terminal seta of P1 exopod-3 (arrowed in Fig. 8D) shorter than outer distal spine. Terminal setae of exopod-3 and endopod-2 without setule comb at tip. Median row of small setules on coxa of P2–P4 (Fig. 8E) slightly more proximal in position than in *T. montagni*.

P5 (Fig. 8F). Baseoendopodal lobe and exopod 6 times longer than wide. Distal inner seta on endopodal lobe shorter (in absolute length) than proximal inner seta.

Male.—As female except for urosome, antennule, P5 and P6.

Body length 0.45–0.52 mm (\bar{X} 0.48 mm, $n = 8$) and slightly more slender than female. Urosomites-2 and -3 completely separate.

P5 (Fig. 7C). Exopod 4 times longer than wide (more slender than in *T. montagni*). Outer seta on endopodal lobe not reaching distal margin of exopod and only slightly shorter than inner seta.

Etymology.—The species is dedicated to

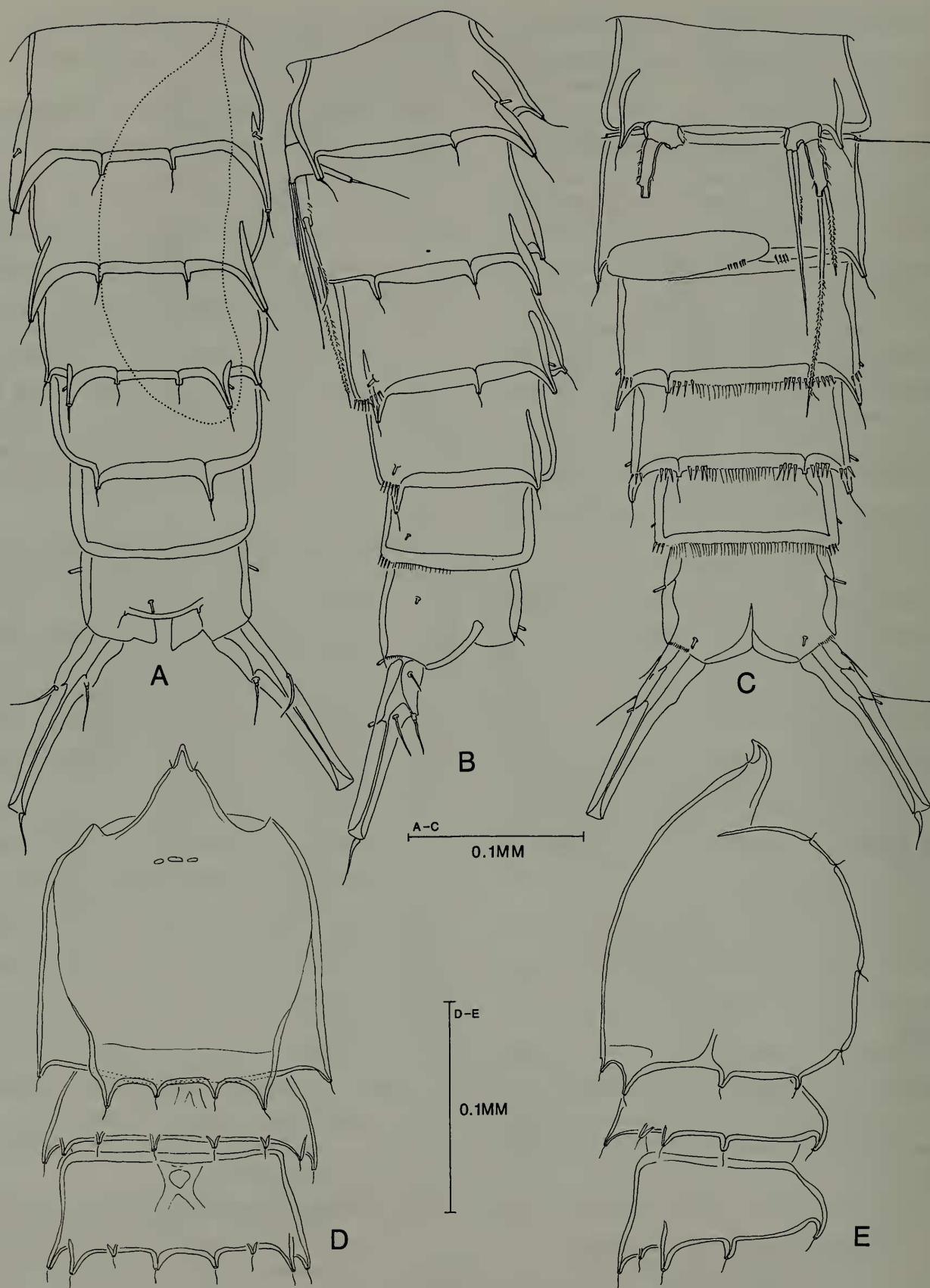


Fig. 6. *Triathrix montagni* new species, male urosome A, dorsal view; B, lateral view; C, ventral view. *Triathrix kalki* new species, female copepod V cephalothorax and first two free prosomites, D, dorsal view, E, lateral view.

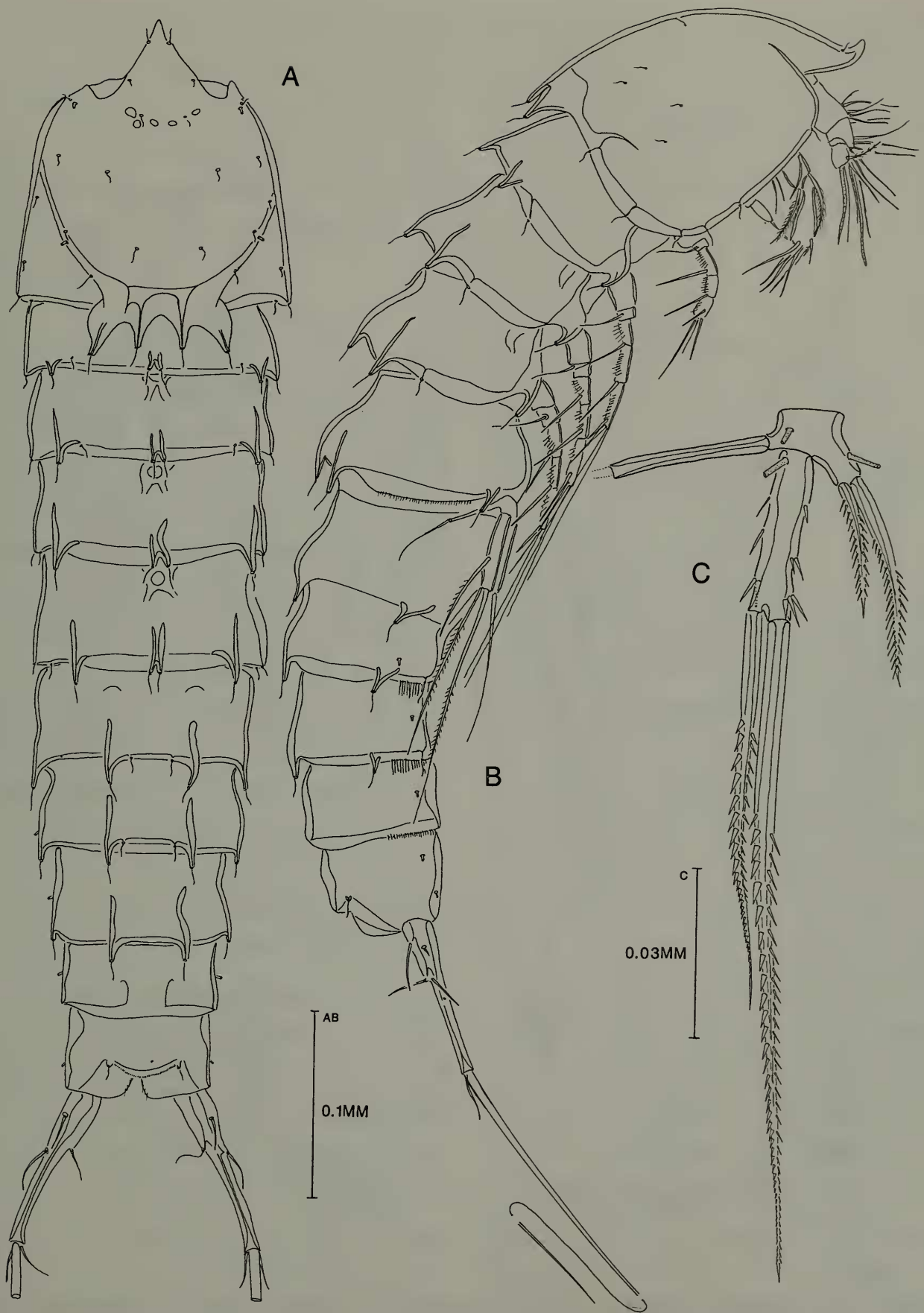


Fig. 7. *Triathrix kalki* new species. A, female body, dorsal view; B, female body lateral view; C, male P5.

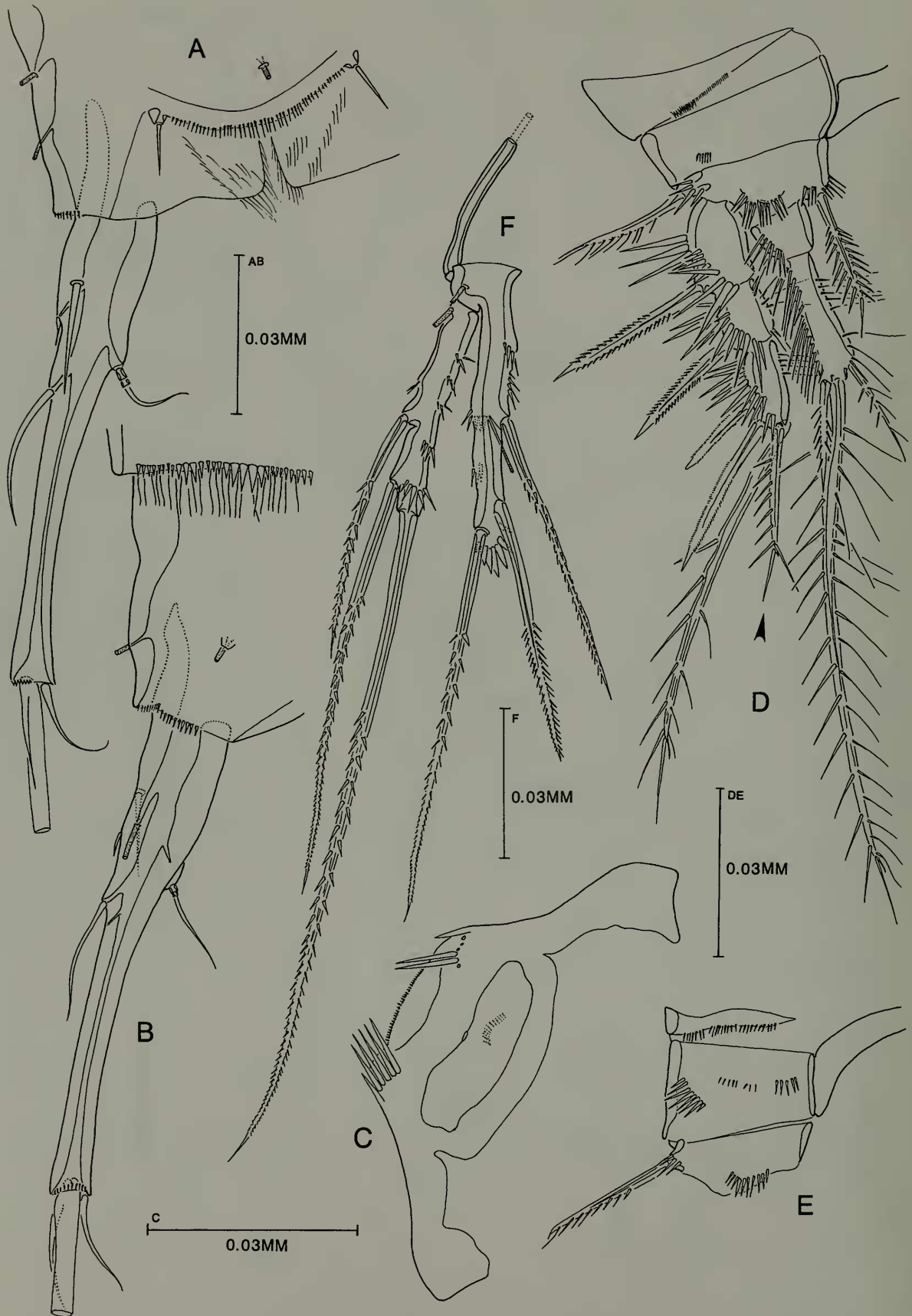


Fig. 8. *Triathrix kalki* new species. A, Female operculum and caudal ramus, dorsal view; B, female caudal ramus, ventral view; C, labrum; D, P1, E, P2 protopod; F, female P5.

our good friend and colleague Mr. Rick Kalke, the leader of the team engaged in the analysis of meiofauna samples from the GOMEX project.

Variation.—Amongst the 13 adult specimens examined there was no variation in the structure and proportion of the appendages or the major features of the body ornamentation.

Discussion

The specimens described above can be placed within the Cletodidae on the basis of the following combination of characters: well defined somites with no hyaline frills but with sensilla and socles on the posterior border; an operculum with a pair of associated sensillum-bearing socles; an antennule which is 5-segmented in the female and 6-segmented in the male; a 1-segmented antennary exopod with at most three setae; rami of the mandible and maxillule fused to the basis; a maxilla with two syncoxal endites; a chelate maxilliped without setae on the basis; the P1 with a 2-segmented endopod in which endopod-2 is much longer than endopod-1; endopod-1 of P1–P4 without an inner seta; P1 and P2 exopod-3 with four setae/spines; the P5s in both sexes not fused medially; the male P6 an asymmetrical plate without armature elements.

Gee (1994) and Gee & Huys (1996) regard the structure of the antenna to be significant in phylogenetic considerations within the Cletodidae. The antenna of the above species (and of *E. nicobarica*) is the most primitive condition found in the family with two setae on the abexopodal margin of the allobasis and a 1-segmented exopod bearing three setae, two on the distal margin and one on the lateral margin. *Limnocletodes* also retains the primitive structure of the antennary exopod but has lost one seta on the abexopodal margin of the allobasis. In the original description of *Acrenhydrosoma perplexa*, Scott (1899) illustrates (plate XI, fig. 15) an exopod with

three setae but these are not homologous with the above because there is only one seta on the distal margin and two setae on the lateral margin. Fiers (1996) is of the opinion that the proximal lateral seta may have been confused with a large spinule, especially in the light of the fact that the other two species of *Acrenhydrosoma* Lang (see Lang, 1965 and Schizas & Shirley 1994) have only one terminal and one lateral seta. All other genera within the Cletodidae have either (a) a well developed exopod with two setae (one distal and one lateral) and one or no setae on the abexopodal margin of the allobasis; or (b) a small cylindrical exopod with one seta and with two or one setae on the abexopodal margin of the allobasis.

Although the structure of the antenna in the species described in this paper is plesiomorphic they are placed in a separate genus on the basis of the following autapomorphies: A chitinous plate with four socles on the posterior margin of the cephalothorax. Most genera of cletodid usually have more than four socles arranged around the margin of the cephalothorax but in no species has a chitinous extension to the cephalothorax been described; No socles on the preanal somite. The arrangement of socles on the urosomites has not always been accurately recorded but for all species and genera that we have examined in detail there are always two non-sensillum bearing socles on the posterior border of this somite; A median tube pore on the operculum. The presence of a pore in this position has not been recorded before in the Cletodidae but again this could be the result of lapses in observation or resolution of microscopes used by previous workers; Seta I of the caudal ramus inserted posterior to seta II. In all other genera in the family, where the condition is known, seta I and seta II arise in very close proximity on the lateral margin of the ramus; The maxillary coxal endite with only 1 seta. For many genera and species of Cletodidae the mouthparts are unknown. However, amongst those that are known, there are two

setae on the coxal endite, except in species of *Enhydrosoma* where the coxal endite is fused to the basis and in *Cletodes millerorum* Hamond, 1973 and *C. pseudodissimilis* Coull, 1971; Maxillary basal complex with eight setae; three on the distal endite, two on the proximal endite, one representing the endopod and two the exopod. It is thought that the primitive condition in the family is 10 or 11 setae on the basal complex, (six or seven on the basal endites and two each representing the exopod and endopod). This is the condition found in *Cletodes*, *Interkletodes* Fiers, *Strongylacron* Gee & Huys and *Schizacron* Gee & Huys. In *Enhydrosoma*, *Enhydrosomella* Monard, *Kollerua* Gee, *Stylicletodes* Lang and *Acrenhydrosoma* (referred to below as the *Enhydrosoma* group) there is a maximum of six setae on the basal complex (four on the basal endites and one each representing the exopod and endopod).

In addition to the above autapomorphies, the genus *Triathrix* is also characterized by the following features: The sharply pointed, triangular rostrum. The phylogenetic significance (and polarity) of this character is difficult to assess but no other cletodids have a rostrum shape identical to these species and there is evidence (Gee & Huys, 1996) that the rostrum has a characteristic shape in each genus; A mandibular palp with five setae. The primitive condition in the family is six setae on the mandibular palp (two on the inner, three on the distal and one medially on the outer margin), found in some species of *Cletodes*, *Interkletodes* and *Monocletodes*. *Triathrix* has lost the seta on the outer margin, as has *Strongylacron* and other species of *Cletodes* with five palp setae, except *C. millerorum*, which appears to have lost the proximal seta on the inner margin. *Enhydrosoma curticauda* Boeck, 1872, the remaining three species of *Cletodes*, *Schizacron* and *Acrenhydrosoma maccalli* Schizas & Shirley, 1994, have four setae on the palp, all having lost the seta on the outer margin and one on the distal margin. All other genera or species where the

condition is known, have three setae on the palp, the additional lost seta being the proximal seta on the inner margin; Proximal maxillary syncoxal endite with two armature elements. The primitive condition in the family is three elements on both syncoxal endites and is found in most species where the condition has been reliably reported. In a number of species of *Enhydrosoma* there are two elements on the distal endite but, except in *Cletodes reductus* Moore, 1977 there are no reliable reports of two elements on the proximal endite; Maxillary allobasal endite with a spine and two setae. Again the primitive condition within the family is a spine and three setae on this endite although all genera in the *Enhydrosoma* group appear to have the *Triathrix* condition; The two setae representing the maxillary endopod are not fused at the base. This is probably the primitive condition in the family and, as far as we know, the basal fusion of these two setae is only found in genera in the *Enhydrosoma* group; Maxillipedal coxa without a seta. Most genera in the family have retained the seta on the coxa but it has been lost in a large number of the species at present placed in *Enhydrosoma* (including the type species); The shape of the female P5 in which the baseoendopodal lobe and the exopod are rectangular in shape and equally long. Only in *Stylicletodes* is the P5 similarly shaped but in this genus there are four or five setae on each ramus compared to only three in *Triathrix*. The rami of the female P5 in *Strongylacron* and *Schizacron* are equal in length and bear three setae but are well separated (giving the limb a characteristic U-shape) and the exopod is fused to the baseoendopod. The female P5 exopod in most species of *Cletodes* is long and rectangular but always bears five setae and the endopodal lobe is usually much reduced. Within the family, the morphology and setal arrangement of the P5 in both sexes are important in defining generic boundaries and are undoubtedly of great phylogenetic significance (Fiers, 1996) but at the moment

the relationships of these characters are difficult to understand; No sexual dimorphism on swimming legs. Within the Cletodidae, sexual dimorphism, when present, is found on the P3 endopod, although in three species of *Enhydrosoma* (*E. longifurcatum* Sars, 1909, *E. latipes* (A. Scott, 1909) and *E. pericoense* Mielke, 1990) it is also found on the P3 exopod. The range of sexual dimorphism on the P3 endopod, its origins and homologies are discussed in detail by Gee (1994), Gee & Huys (1996) and Fiers (1996). Briefly however, the former two authors regard the 3-segmented P3 endopod in the male of *Cletodes*, *Strongylacron*, *Schizacron* and *Enhydrosoma curvirostre* (T. Scott, 1894) as a development (apomorphy) from an originally 2-segmented ramus (plesiomorphic condition) and interpret the absence of sexual dimorphism in some species of *Cletodes*, *Interkletodes* and *Monocletodes* as a secondary loss of sexual dimorphism. The latter author, on the other hand regards the 3-segmented ramus on the male P3 as the plesiomorphic condition and absence of sexual dimorphism as the most advanced state.

We have not examined the single known specimen of *E. nicobarica* which is a male copepodid V and the description of Sewell (1940) does not detail the structure of the mouthparts. Nevertheless, the shape of the rostrum, the setation of the antennal exopod and the caudal ramus, and the structure of the juvenile P5, all suggest that this specimen is a juvenile *Triathrix*. There is no evidence of the posterior extension to the cephalothorax in the drawing of the dorsal view of the body of *E. nicobarica* (Sewell, 1940 fig. 85A). However, it is known (F. Fiers, pers. comm.) that one of two further new species belonging to this genus from Campeche Bank, Yucatan Peninsula, southern Gulf of Mexico, has an even smaller dorsal extension than that of *T. kalki*. Further, an examination of the copepodid V specimens in our sample of *T. kalki*, shows that the posterior extension of the cephalothorax is not developed in the last juve-

nile stage (Fig. 6D–E). In addition, it should be noted from Fig. 6D–E, firstly, that there are eight socles on the cephalothorax and ten on the free prosomites in copepodid V rather than the four and six respectively found in the adult and, secondly that the median dorsal socles are well separated in copepodid V rather than fused as in the adult of this species. Thus, it is clear that the distinctive body features of the species described in this paper may only appear in the adult and that the copepodid V stage is the same as that drawn by Sewell (1940) for *E. nicobarica*. Further, Sewell illustrated the P1 endopod-2 of *E. nicobarica* with only two elements (Sewell, 1940, fig. 85F) and noted that the inner distal element of P2 exopod-3 was a spine-like element (rather than a normal seta as in *T. montagni* and *T. kalki*). Developmental studies on Cletodidae (Fiers, 1991, 1996) indicate that all setae present in the adult are also present in copepodid V but may differ slightly in appearance. Thus the absence of an inner seta on P1 endopod-2 in *E. nicobarica* clearly distinguishes it from the two species described above but the form of the distal elements on P2-endopod-3 may be just a juvenile precursor of a normal seta and not a distinguishing feature. Thus, it is clear that *E. nicobarica* should be transferred to the new genus *Triathrix* as *T. nicobarica* new combination.

Finally, *Triathrix* appears to be limited in its distribution to the Indo-Pacific Oceans and the western Atlantic with three species known to inhabit the Gulf of Mexico region east of the central American isthmus, one the Californian Pacific coast and one the Indian Ocean. Woodring (1966) presents evidence from the fossil molluscan record suggesting that the whole of the Caribbean area and tropical eastern Pacific formed a single biogeographic province during the Miocene. Jones & Hasson (1985) suggest that the Central American isthmus gradually emerged from about the time of the late Miocene with final closure occurring in the southern part of the isthmus some three

m.y.a. in the late Pliocene or early Pleistocene. The present known distribution of *Triathrix* suggests that the genus was in existence well before that date and that during more recent times speciation within the Gulf of Mexico region has been greater than that in the eastern Pacific region. However, it must be remembered that the harpacticoid copepod fauna of the Caribbean and Central American region is extremely poorly known, especially for sublittoral communities. Therefore the present known distribution of species on either side of the isthmus may be more a function of sampling effort than the pace of evolution.

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Literature Cited

- Fiers, F. 1991. Three new harpacticoid copepods from the Santa Maria Basin off the Californian Pacific coast (Copepoda, Harpacticoida).—*Beaufortia* 42(2):13–47.
- . 1996. Redescription of *Enhydrosoma lacunae* Jakubisiak, 1933 (Copepoda, Harpacticoida); with comments on the *Enhydrosoma* species reported from West Atlantic localities, and a discussion of cletodid development.—*Sarsia* 81:1–27.
- Gee, J. M. 1994. Towards a revision of *Enhydrosoma* Boeck, 1872 (Harpacticoida: Cletodidae sensu Por); A re-examination of the type species, *E. curticauda* Boeck, 1872, and the establishment of *Kollerua* gen. nov.—*Sarsia* 79:83–107.
- , & R. Huys. 1996. An appraisal of the taxonomic position of *Enhydrosoma buchholzi* (Boeck, 1872), *E. bifurcarostratum* Shen & Tai, 1965, *E. barnishi* Wells, 1967 and *E. vervoorti* Fiers, 1987 with definition of two new genera (Copepoda, Harpacticoida, Cletodidae).—*Sarsia* In press.
- Huys, R., J. M. Gee, C. G. Moore, & R. Hamond. 1996. Marine and brackish water harpacticoid copepods Part 1. Synopses of the British Fauna (Ed. R. S. K. Barnes & J. H. Crothers), Field Studies Council Press, UK. 51:1–352.
- Hyland, J., D. Hardin, I. Creclius, D. Drake, P. Montagna, & M. Steinhauer. 1990. Monitoring long-term effects of offshore oil and gas development along the southern California outer shelf and slope: background environmental conditions in the Santa Maria Basin.—*Oil and Chemical Pollution* 6:195–240.
- Jones, D. S., & P. F. Hasson. 1985. History and development of the marine invertebrate faunas separated by the Central American Isthmus. Pp. 325–356 in F. G. Stehli & S. D. Webb, eds., *The Great American Biotic Interchange*. Plenum Press.
- Lang, K. 1948. Monographie der Harpacticiden I: 1–896, figs 1–361; II: 897–1682, figs. 362–607, maps 1–378. Håkan Ohlsson, Lund.
- . 1965. Copepoda Harpacticoida from the California Pacific Coast.—*Kungliga Svenska VetenskapsAkademiens handlingar* 10:1–560.
- Montagna, P. A. 1991. Meiobenthic communities of the Santa Maria Basin on the California continental shelf—*Continental Shelf Research* 11: 1355–1378.
- , & D. E. Harper Jr. 1996. Benthic infaunal long-term response to offshore production platforms.—*Canadian Journal of Fisheries and Aquatic Sciences*. In Press.
- Por, F. D. 1986. A re-evaluation of the family Cletodidae Sars, Lang, (Copepoda, Harpacticoida). In G. Schriever, H. K. Schminke, & C.-T. Shih eds., *Proceedings of the Second International Conference on Copepoda*, Ottawa, Canada, 13–17th August, 1984.—*Syllogeus* 58:420–425.
- Schizas, N. V., & T. C. Shirley. 1994. *Acrenhydrosoma maccalli*, a new species from Auke Bay, Alaska (Copepoda, Harpacticoida).—*Crustaceana* 67:329–340.
- Scott, T. 1899. Notes on recent gatherings of micro-Crustacea from the Clyde and the Moray Firth.—17th Annual Report of the Fisheries Board of Scotland for 1898, Part III: 248–273.
- Sewell, R. B. S. 1940. Copepoda, Harpacticoida.—*The John Murray Expedition 1933–34, Scientific Reports*, British Museum (Natural History) 7: 117–382.
- Woodring, W. P. 1966. The Panama land bridge as a sea barrier.—*Proceedings of the American Philosophical Society* 110:425–433.